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DEFOLIATION AS A RESULT OF DECLINE IN THE ABSOLUTE PHOTIC RATION (SUMMER DEFOLIATION)

[Following is a translation of an article by Julius Wiesner in the German-language periodical Berichte der Deutschen Botanischen Gesellschaft (Reports of the German Botanical Society), Vol 22, 1904, pages 64-72.]

Nothing is seemingly simpler than the falling of leaves that takes place in plants, especially woody plants. Deeper penetration into the study of defoliation, however, has shown that not only the anatomical changes that lead to the shedding of the leaves but also the causes of partial or complete defoliation of plants are extremely varied.

I shall restrict myself here to a brief presentation of a new external cause of defoliation, but one whose importance can hardly be doubted. In a later article I shall discuss in detail the subject dealt with here and other questions concerning defoliation.

For several years I have made the observation that at the beginning of the summer numerous deciduous woody plants shed an often not inconsiderable part of their foliage. Day by day or in short periods of a few days leaves fall from the trees which are visibly dying or even completely dead.

I first observed this phenomenon in Acer negundo. About 21 June a slight shedding of leaves begins, which hardly increases toward fall, but later changes in an almost sudden rise into the normal autumnal defoliation. Rendered alert by this phenomenon, I have also observed this form of defoliation in other woody plants. I have found it in other species of maples, in the horse chestnut, and in numerous other deciduous woody plants. The behavior is essentially the same as in Acer negundo; the shedding of leaves increases either not at all or barely perceptibly, and later goes over almost suddenly into the autumnal defoliation.

It will be seen immediately that the form of defoliation with which we are concerned here has nothing to do with that defoliation of woody plants that sets in as a result of summer drought and is then typical of the species concerned or of a specific local variety, or is often observable in the form of a partial defoliation during the hot summer months in ordinary deciduous plants.

Both these forms of defoliation take place in the summer, but while that with which we are dealing here either lasts throughout the summer or runs its course in a portion of the summer independent of heat and dryness (especially dryness of the ground), determined so to speak only astronomically, the other form occurs only during a brief, hot period of time within the summer, characterized by great dryness (especially of the ground). The former, while it takes no small amount of foliage from the tree, always does so only in small batches, while the latter takes away equally large quantities of leaves all at once, so to speak, within a short span of time.

Since these two forms of defoliation occurring during the summer differ not only with respect to the period in which they take place but also in other respects, and since moreover, as we shall see, they owe their occurrence to quite different causes, it is quite advisable to distinguish them by different names. I should like to designate the former type as summer defoliation and the latter as heat defoliation.

One great difference between these two forms of defoliation consists in the fact that in "summer defoliation" the innermost, least well-lighted leaves are dropped, while in "heat defoliation" it is precisely the peripheral leaves, exposed to the strongest sunlight, that fall prey to defoliation, obviously primarily by reason of an excessive transpiration, with which the supply of water from the trunk cannot keep pace; perhaps the killing of the leaf also takes place because of other effects of the direct sunlight.

I shall discuss only that form of leaf drop here which I have given the name of "summer defoliation."

As my studies of leaf drop coincided with those concerning the light utilization of plants [see Note], I arrived at an understanding of the cause of this type of defoliation sooner than perhaps would otherwise have been the case.

[Note] My studies concerning the light utilization of plants are summarized in the new edition of my Biologie der Pflanzen (Plant Biology), Vienna, 1902, page 325.

It has been found with perfect certainty that the cause of summer defoliation lies in the altered light utilization which in plants with light-sensitive foliation sets in theoretically shortly after the coming of astronomical summer, or, more precisely, when the highest noon elevation of the sun and consequently the greatest amount of daylight is past in the course of the year.

On 21 June the sun reaches its highest noon elevation, and from then on, clear weather of course assumed, the daily light intensity declines. Now if the relative light ration, i.e. the ratio of total light intensity to the light intensity to which the plant or an above-ground organ of it is exposed, remains nearly constant, as the summer advances the absolute light ration for each plant declines. The loss of leaves that sets in in consequence of this regulates, as is easy to see, the minimum of the relative light ration.

For summer defoliation to show up in clearly recognizable form, the woody plants concerned must possess leaves which immediately die when carbon dioxide assimilation stops. Let me present two characteristic examples of this.

If the leaves of Acer negundo are prevented from assimilating carbon dioxide and water by too low a light intensity or as a result of complete darkness, even under otherwise favorable conditions they die and fall from the tree. This takes place after only a few days. The time of falling varies with temperature and atmospheric humidity.

On the other hand a sprig of laurel even in complete darkness stays fresh and green for weeks and even months. This is also true of the quite normally rooted plant. A sprig of laurel that I kept in a space with 100% humidity for 2 1/2 months (at medium temperature) remained fresh the whole time and did not lose a single leaf. The difference between this sprig and others growing normally on the trunk in the light was merely that it lost a little chlorophyll and so appeared a little lighter green than the normally growing branches.

Acer negundo is subject to a very noticeable "summer defoliation," while the laurel exhibits either no "summer defoliation" at all or a barely discernible one. The relatively very great defoliation of the laurel which does take place in the summer is due not to a decline in the intensity of daylight but, as I shall show further on, to quite other causes.

"Summer defoliation" will occur more markedly in woody plants the greater the sensitivity of their foliage to darkness, i.e. the sooner their foliage dies after cessation of carbon dioxide assimilation. As this sensitivity decreases

the summer defoliation declines in intensity, dropping e.g. in the laurel to zero or very near zero.

As examples of marked summer defoliation let me adduce two series of experiments that were carried out along with many others in the summer of 1903. They have to do with two woody plants which at the beginning of the summer (21 June) had not yet completed the development of their foliage.

The trees used in the experiments were so situated that their falling leaves could not be carried away by the wind, so that it was possible to effect a precise determination of the daily fall of leaves. One of the trees was a horse chestnut (Aesculus hippocastanum), the other a species of maple (Acer dasycarpum). The former had a height of 7.20 meters and a crown diameter of about 4 m, the latter a height of 8.80 m and a crown diameter of about 5.45 m. The horse chestnut had almost a free exposure to the southwest, the maple to the southeast.

From 18 June on the trees were closely checked day by day for leaf fall. The first leaves of the horse chestnut fell on 24 June, and from then until complete defoliation not a day went by on which no leaves fell. In the case of the maple the leaf drop began on 29 June, but otherwise it behaved exactly like the horse chestnut. In June the maple lost 7 leaves, the horse chestnut 37.

The fallen leaves were of course counted daily, but in order to shorten my account as much as possible, I show in the accompanying table the number of fallen leaves for periods of 10 (or 11) days. [See page 5.]

I am reserving a detailed presentation of the defoliation of these two trees, in which both the daily fall of leaves and the daily observations of meteorological data, which are particularly worth considering, will be shown, for the article announced above.

But even from the summary data given here it can be seen that the "summer defoliation" does not change gradually into the autumnal defoliation, but suddenly, as has been mentioned above, inasmuch as all the factors that condition the autumnal defoliation work together at once. It will also be seen that the summer defoliation carries away not inconsiderable quantities of leaves, -- in the case of Acer 10%, in the case of Aesculus about 30% of the entire foliage.

There are woody plants with shade-sensitive foliage whose "summer defoliation" begins not at the beginning of summer, but later. These are trees that complete their foliation

Date	Number of Fallen Leaves Acer	Aesculus
1-10 July	121	155
11-20 "	167	229
21-31 "	98	187
1-10 August	120	188
11-20 "	36	118
21-31 "	128	40
1-10 September	179	15
11-20 "	116	26
21-30 "	412	28
1-10 October	3062	461
11-20 "	3043	881
21-31 "	2343	798
1-10 November	2749	345
11-20 "	1293	927
21-29 "	317	127*
Total leaves shed	14191	4562

*The last leaves fell from both trees on 29 November. Until then the trees had not been exposed to frost.

before the beginning of summer. A well-known example of this is the beech, in which foliation takes place very rapidly and is very soon completed. According to my observations the beech (Fagus silvatica) around Vienna is completely leafed out within 14 days to 3 weeks and has thus completed the formation of its foliage leaves. In such plants, which have stopped their leaf formation long before the beginning of summer, the summer defoliation begins very late, not until the noon elevation of the sun has fallen below that at which the leaf formation was brought to completion. Thus for example if the leaf formation was brought to completion by the beginning of May (noon elevation of the sun in the vicinity of Vienna nearly 57°), summer defoliation does not begin until the first third of August.

Detection of summer defoliation will always take a certain alertness, for the causes of leaf drop are extremely varied. Not infrequently it will happen that within the normal, light-dependent "summer defoliation" there will be a heat

defoliation. In the same way a long period of rains may bring about a leaf drop independent of the "summer defoliation." Then, too, there may be a leaf drop even before 21 June, either because of a long period of overcast skies or as a result of damage to the leaves [see Note], and so on.

[Note] Wiesner, "Studies of the Autumnal Defoliation of Woody Plants," Sitzungsberichte der Wiener Akademie (Minutes of the Vienna Academy), 1871.

Trees whose foliage is little sensitive to shade either do not undergo "summer defoliation" or, if such a phenomenon does occur, are subject to it only to a very slight degree. The leaves of woody plants whose foliage is little sensitive to shade endure even complete darkness for a long time without dying and without falling from the tree. In these plants the minimum photic ration drops to an extraordinarily low value, so that it is understandable that the declining light intensity of summer exerts no influence or only a minimal influence on them.

As an example let me cite the laurel. It does lose a great many leaves in the summer, but not in consequence of the declining light intensity; it is rather, as I have found, in a quite different and as far as I know a previously unobserved way. The great leaf drop of the laurel falls in the period of budding, or in this area in the months of June or July or both. One laurel that I observed in Vienna, cultivated in a large tub and about 2 meters high, with, by the way, 3800 leaves, lost 580 leaves during budding, and then in August lost only 73 leaves, in September 52, in October 14, in November (in a cold greenhouse; from May through October the shrub was kept outdoors) 13, and in December 9. Even in the months from January to May the number of leaves lost was quite small in comparison to that during budding.

No doubt there are numerous other evergreen woody plants in which a heavy partial defoliation occurs in consequence of the onset of budding, just as in the laurel. I have made the observation on the myrtle and some other evergreen plants that if during the period of their vegetative rest they are brought out of the cold greenhouse into a tempered dark room, after a time an intensive budding sets in, followed by an intensive defoliation. Before the budding either no leaf drop had occurred at all or it was much slighter than after the onset of budding. In these plants it is precisely by budding that the conditions are created that lead to the organic shedding of leaves.

Laurel and other woody plants little sensitive to shade and of similar habit have no "summer defoliation" or only an insignificant one.

Absence or slight degree of "summer defoliation" also seems to occur with those woody plants in which the minimum photic ration is very high, e.g. in the larch (Larix decidua) and the birch (Betula verrucosa), whose photic ration at a moderate elevation in Lower Austria in natural habitats drops from 1 down to 1/5 or even 1/9. But these are very high minima of light utilization compared e.g. with the box tree, whose minimum is near 1/100. And the minimum for the laurel is much lower yet; it is in fact so low that it cannot be measured with our present means.

In Laurus it is the insensitivity of the foliage to darkness, in the larch and the birch the relatively thin foliage that rule out "summer defoliation" or reduce it to a minimum.

Summary

1. Foliage leaves which are prevented from assimilating carbon dioxide die after varying lengths of time and in the case of woody plants separate as a rule from the trunk. This is the chief reason that leaves kept dark die after a longer or shorter time and separate from the trunk. Many deciduous trees shed their foliage in a few days when cut off from light, while the foliage of the laurel remains alive for many weeks under these conditions and does not separate from the trunk.

2. Trees with foliage sensitive to shade generally undergo a partial defoliation during the summer which is attributable to the fact that the decline in daily light intensity following the beginning of summer brings about a reduction of the (absolute) photic ration of the plants concerned below the minimum, and this in turn brings about separation of the leaves.

3. "Summer defoliation," that is the defoliation occurring in the summer in consequence of the decline in absolute photic ration, often takes from the trees up to 20% of their foliage, but sometimes less (8% has been observed) and sometimes more (up to 30% has been observed).

4. Trees whose foliation extends into the summer, if they are sufficiently sensitive to shade, have leaf drop throughout the summer.

5. The "summer defoliation" of those trees whose foliation is completed in the spring does not begin until the noon solar elevation has again reached the value at which the foliation of those trees was completed (beech).

6. Trees with low sensitivity to shade have either no "summer defoliation" or a minimal one (laurel).

7. Trees with very high minimum photic ration also show either no "summer defoliation" or a very slight one.

8. The "summer defoliation" described ~~above~~ is not to be confused with "heat defoliation," which sets in as a result of drought and heat. ~~The former~~ removes the leaves least exposed to sunlight, the latter those most exposed; or in other words the former the innermost, the latter the outermost leaves of the tree's foliage.

The expression "summer defoliation" in the meaning in which it is used above would seem to be quite unambiguous and can give no occasion for confusion with other forms of leaf drop.

I will freely admit, however, that the expression is not happily chosen in that still other forms of defoliation occur precisely in the summer, such e.g. as "heat defoliation," the defoliation also mentioned above which sets in as a result of budding, and still others.

But in this short report I do not intend to open up the question of the terminology of defoliation.
